Cupiennius (Araneae, Ctenidae): Biology and sensory ecology of a model spider

Cupiennius (Araneae, Ctenidae): Biología y ecología sensorica de una araña modelo

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Abstract: *Cupiennius* is a genus of hunting or wandering spiders typical of Central America including the Golfo Dulce region, which do not live in a silken web or build a web to catch prey. Instead, a prominent feature of their biology is a close association with particular dwelling plants on which they hide during the day and prey and court at night. The complex behavioural patterns of *Cupiennius* rely on an armament of exquisite sensors tuned to the specific needs in the spiders' specific environment. After a short introduction to the taxonomy, distribution and habitat, a few examples are given to show how closely spider sensory systems mesh with spider behaviour in the natural habitat. A key for the genus *Cupiennius* is provided by a companion paper (BARTH & CORDES).

Key words: hunting spider, sensory ecology, spider-plant interaction, *Cupiennius coccineus*.

Resumen: El género *Cupiennius* reune a un grupo de arañas de caza o errantes típicas de América Central, incluyendo la región de Golfo Dulce, que no viven en una telaraña o construyen una tela para atrapar a su presa. En su lugar, una importante característica de su biología, es una estrecha asociación con plantas particulares que le sirven de morada, donde se ocultan durante el día y cazan y cortejan en la noche. Los complejos patrones de comportamiento de *Cupiennius* dependen de una serie de extraordinarios sensores, sintonizados con las necesidades particulares de las arañas en ambientes específicos. Después de una corta introducción a la taxonomía, distribución y hábitat, se entregan algunos ejemplos para mostrar como los sistema sensoriales de las arañas se relacionan con el comportamiento de la araña en el hábitat natural. Una clave para el género *Cupiennius* es entregada por el trabajo siguiente (BARTH & CORDES).

Palabras clave: araña cazadora, ecología sensorial, interacción araña-planta, *Cupiennius coccineus*.

Spiders

It may be that some of the readers of this chapter share a kind of reservation against spiders with some other people. It should be said at the outset that in most cases this uncomfortable feeling about spiders is very superficial and easy to cure simply by learning some basics about their varied and complex behaviour. Spiders are wonderful creatures, shaped by some 400 million years of evolution and well matched to the conditions of their habitat as is evident from their evolutionary success.

The spiders introduced in this chapter are special ones. The reason for their distinction is that they have gained a good reputation as experimental animals and indeed the status of a model animal in a number of laboratories world-wide; in many respects, they are the most widely researched among all spiders (MELCHERS 1963, BARTH 2001, 2002).

Taxonomy

It was Eugène Simon, the famous French arachnologist, who established the genus *Cupiennius* in 1891 (SIMON 1891, 1897, 1898). In 1984, 93 years later, we revised the genus (LACHMUTH et al. 1984), examining 533 adult animals from the arachnological collections of museums throughout the world as well as numerous live specimens observed by us in their Central American habitat. The outcome of this effort was a reduction of the then 21 nominal species to seven. Three of these species are large-bodied with leg spans of up to 10 cm and above (Fig. 1): *C. salei* KEYSERLING 1877, *C. getazi* SIMON 1891 and *C. coccineus* F. PICKARD-CAMBRIDGE 1901. The remaining four species are the smaller ones with leg spans of up to about 4 cm: *C. granadensis* KEYSERLING 1877, *C. foliatus* F. PICKARD-CAMBRIDGE 1901, *C. cubae* STRAND 1910, and the new species *C. panamensis* LACHMUTH et al. 1984. In the meantime the

Fig. 1: **The three large species** of the genus *Cupiennius*: *C. salei* (Keyserling 1877), *C. coccineus* (F. Pickard-Cambridge 1901) and *C. getazi* (Simon 1891). The photographs show adult female and male animals in dorsal and ventral view. Note the orange and grey colour varieties of *C. getazi* females. The body lengths excluding the legs for female and male, respectively, are 3.3 and 3.2 cm for *C. salei*, 2.8 and 2.9 cm for *C. coccineus*, and 2.8 and 2.3 cm for *C. getazi*. Scale bars represent 1 cm (modified from Barth 2002).
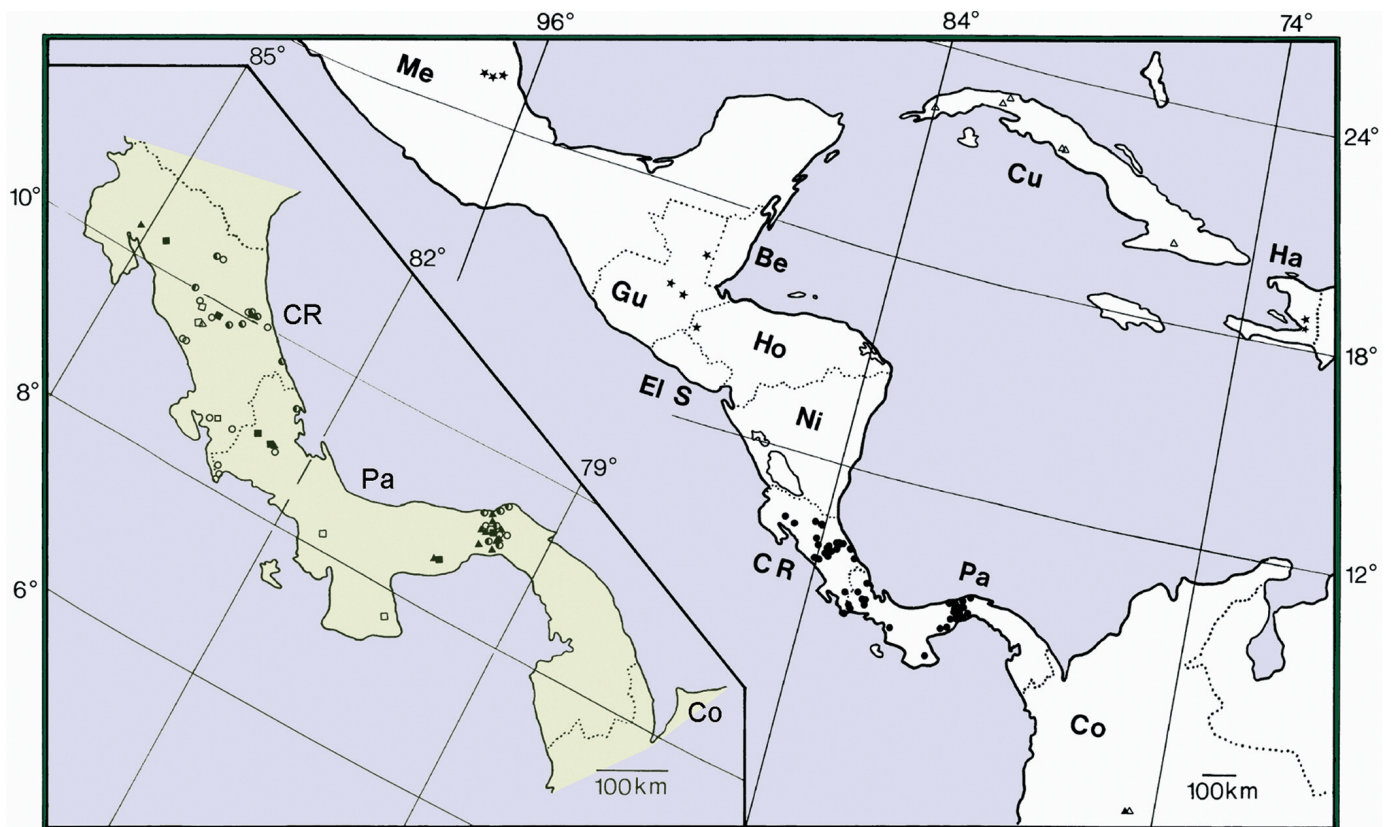
Fig. 2: **Geographical distribution** of seven species of *Cupiennius*. *C. remedius* has so far been reported only from Guatemala (BARTH & CORDES 1998), *C. vodou* sp. nov. from Haiti (BRESCOVIT & POLOTOW 2005), and *C. chiapanensis* from Chiapas, Mexico (MEDINA SORIANO 2006). *C. celerrimus* has been recently been found again in Brazil (Amazonas; BRESCOVIT & VON EICKSTEDT 1995). O *C. coccineus*, ◖ *C. getazi* , * *C. salei*, ■ *C. panamensis*, □ *C. foliatus*, ▲ *C. granadensis*, △ *C. cubae*. Be Belize, Co Colombia, Cu Cuba, El S El Salvador, Gu Guatemala, Ha Haiti, Ho Honduras, Me Mexico, Ni Nicaragua, Pa Panama (modified from BARTH et al. 1988).

genus has grown by 4 more species, all smaller than the three big species: *C. remedius* BARTH & CORDES 1998, *C. celerrimus* SIMON 1891 (redescribed by BRESCOVIT & VON EICKSTEDT 1995), *C. vodou* BRESCOVIT & POLOTOW 2005, and the most recent addition *C. chiapanensis* MEDINA SORIANO 2006.

The most intensively studied among all these species is *C. salei* (BARTH 2001, 2002); it was first described as *Ctenus Saléi* by Count Eugen Wilhelm Theodor von Keyserling in the 1877 Proceedings of the Zoological-Botanical Society of Vienna. But the similarities of this species in particular to the other two large species *C. getazi* and *C. coccineus* are very obvious. A key for the identification of the different species of the genus except *C. vodou* and *C. chiapanensis* is found in the companion paper by BARTH & CORDES. The majority of species were successfully bred and raised in the laboratory and can therefore be categorised not merely as morphospecies but also as biospecies.

Geographic distribution and habitat

Cupiennius mainly is a Central American genus, its distribution including the Caribbean with Cuba, Haiti

and Jamaica as well as parts of the North of South America (Fig. 2). Judging from our own searches and information given in the literature and in the arachnological collections so far all species of the genus except the following were found in Costa Rica (see also PLATNICK 2007, The World Spider Catalogue, Version 7.5): *C. vodou* (Haiti, Hispaniola), *C. chiapanensis* (Chiapas, Mexico), *C. celerrimus* (South America), and *C. salei* (from Mexico to Honduras). According to my own experience with *Cupiennius* I suppose that of these species *C. salei* is the one most likely to be living in Costa Rica, but simply has not been searched for carefully enough until now.

Unfortunately no reports of the results of any systematic spider collecting activity in the Golfo Dulce region have yet been published. The two *Cupiennius* species we came across are *C. foliatus* and *C. coccineus* (Fig. 3). A serious search is overdue and will bring to light additional species of the genus.

However, with *C. coccineus*, one of the large species, characteristic features of habitat and behaviour can well be described for the large species at least, to which it belongs.

Fig. 3: *Cupiennius coccineus*. Left: female on a bromeliad, a typical dwelling plant, feeding on a cricket caught during its nocturnal activity period. Right: note brilliantly red undersides of the femora of female.

Dwelling plants, retreats, and microclimate

The way of life of *Cupiennius* and its sensory ecology can only be understood when considering its close relationship to particular plants. All *Cupiennius* species belong to the wandering or hunting spiders and none of them builds a web in order to catch prey. Instead, they spend the day hidden in retreats on plants on which they court, catch prey or moult at night. When searching for *Cupiennius* in the field, the best method is to go out after sunset and to use their typical dwelling plants as signposts: these plants have mechanically strong, unbranched and large leaves which form retreats for the spiders at their bases, effectively open only upward. Such spider shelters are most readily found in the bromeliads, agaves and plants of the banana family (Fig. 4). A list of all the plant species on which *Cupiennius* was found is provided in BARTH (2001, 2002). Prominent *Cupiennius* plant families are the Bromeliaceae, Musaceae, Araceae, Arecaceae and Zingiberaceae. Some plants provide large leaves but no retreats. Remarkably, in such cases, the spiders frequently build a shelter themselves by closing open spaces. Sometimes they spin together adjacent leaves or construct tunnels by bending and rolling up leaves and fastening their ends with silk (Fig. 4) (BARTH et al. 1988). A similar behaviour is seen in females after copulation or when they are already carrying their egg sac (Figs. 4 and 5).

Choosing the right habitat is of fundamental significance for all animals. With their lives so closely bound to plants, *Cupiennius* spiders have to use the right criteria to make their choice. Extensive choice experiments carried out both in the field and in the laboratory (MITTER 1994; review in BARTH 2001, 2002) have demonstrated a preference of monocots to dicots, in particular of those offering a hiding place, which is the most important but not the only criterion for the spider. Remarkably, the spiders optimise their choice of microhabitat by choosing plants with both shelter and prey rather than plants with only one of these advantages. In other words, they perceive and take into account several factors at once instead of orienting themselves by a single environmental parameter and thereby acquiring a whole set of factors automatically.

How about the microclimate? Spiders are not endothermic and their metabolic rate is too low to gener-

Fig. 4: **Typical retreats** on plants which should be used as signposts when searching for *Cupiennius* in the field. (**a**) *C. getazi* female (grey variety). (**b**) *C. salei* female hidden behind a tightly woven silken carpet closing the space between leaves of the pseudostem of a banana plant (*Musa sapientium*). (**c**) Retreat of female *C. salei* with egg sac in the centre of a bromeliad. (**d**) On some plants with large leaves but lacking hideaways, the spiders often build their shelters themselves by spinning together adjacent leaves or bending and rolling up leaves to form tunnels. Note that closing the retreat in the way shown in B and C is only typical of copulated females or females already carrying an egg sac. Otherwise these retreats are usually not modified by spider silk.

Fig. 5: **Reproduction**. (**a**) A couple of *C. coccineus* copulating, taking positions typical of *Cupiennius*: note greyish male upon female facing her posterior end and trying to insert the tip of his bulb (terminal segment of his pedipalp) into the female epigynum to transfer his sperm (photograph E.-A. Seyfarth). (**b**) Shortly after copulation, the female closes her refuge by spinning silken walls. Here a female *C. salei* is seen in her retreat on a banana plant. She will carry her egg sac with her for about 25 days (photograph D.L. Schorkopf). (**c**) Egg sac with its densely woven wall loosened by the female to enable the spiderlings to leave their nursery. (**d**) Spiderlings (body length ca. 2 mm) of a cloud of hundreds close to the egg sac in a tangle of silken threads previously spun by her mother. This tangle is left by the spiderlings after about 9 days when the supply of yolk is used up.

ate their own heat. They also lack the proper musculature for that purpose, differing for instance from a bumblebee with its flight muscles (ANDERSON 1970). Does then *Cupiennius* have an ectothermic way of keeping its body temperature and water content, which is closely related to temperature, within the proper limits? As a nocturnal animal sitting in its retreat during the day, *Cupiennius* is shielded from the sun and heat desiccation. During the day, the average rate of water evaporation is much lower inside than outside the retreat. At night the conditions are practically the same inside and outside. Likewise the relative humidity within the retreat was always found to be above 90% whereas outside the plant it fell to considerably lower values at noon. The retreat is therefore a refuge in a climatic sense as well and helps the spider to conserve water. This is of particular importance for the survival of *Cupiennius* for which even a moderate water loss of 12% to 21% of its body weight is lethal (MITTER 1994). Interestingly, the water loss of *C. getazi* and *C. coccineus* due to evaporation is considerably higher than in other spiders, which underlines the importance of the hiding place and also that of scheduling all activities for the climatically favourable hours of darkness.

The day-night rhythm of the three large species of *Cupiennius* is well studied. When the light intensity has fallen to about 15 lux the spiders turn around and leave their retreat. They do this in precisely the same way day after day at the same time like many bats do – so that one can set one's watch and determine light intensity by observing their behaviour (BARTH & SEYFARTH 1979; SEYFARTH 1980; SCHMITT et al. 1990). One of the advantages of being so strictly nocturnal, in addition to avoiding the heat and low relative humidity of the day, is that most of the prey animals like cockroaches, crickets, earwigs, moths and small frogs are active at night as well, whereas predators of *Cupiennius* like birds, spiderwasps and certain reptiles are day-active. The strict day-night rhythm of *Cupiennius* has an important consequence for the behavioural physiologist too: many behaviours can be elicited much better or even only during the night. Moulting, which is likely to represent the most dangerous hours in the life of a spider, would probably not work at high daytime temperatures when the exuvial fluid would lose its lubricant action because of its rapid evaporation. At many occasions in the field we observed moulting only at night (Fig. 6).

Sensory systems and behaviour

Sense organs are the interfaces between the environment and the central nervous system and therefore also an animal's link between its environment and its behaviour. Understanding the world a spider like *Cupi*

Fig. 6: **Moulting.** A female *C. coccineus* hanging from a bromeliad on her safety thread during the last of the 11 moults which she has to master after having left the egg sac. Note the exuvia on the left (from BARTH 2002).

ennius lives in, therefore, depends to a large extent on an understanding of its sensory organs and their behavioural significance. Importantly, sensory organs and the neural structures that transmit and integrate their signals are not merely transparent windows to the outside world. Instead they are highly selective filters providing a distorted and limited species-specific picture of the world. The goal is never abstract knowledge but survival and reproduction. There have been strong selection pressures on sensory systems assuring that the information an animal obtains from its senses is the information relevant for its species-specific behaviour in its species-specific environment. After four decades of research on the sensory systems of *Cupiennius* (for a review see BARTH 2001, 2002 and 2004), we are now left with fascination regarding both their match with biotic and abiotic factors in their habitat and their "technical" perfection. In the following a few examples will be given to illustrate this.

Vibrations and their reception

Like in many other spiders, among all senses, the mechanical senses are especially well developed in *Cupiennius*. When a *Cupiennius* spider has left its retreat at night and is ready for its nocturnal life at a light intensity below 0.1 lux (which is complete darkness to human eyes) it does not sit in a web but on a plant leaf, waiting for prey. In this situation, sensory information about a cockroach running around on the plant or a moth passing by in flight comes from highly sensitive vi-

Fig. 7: When a *Cupiennius* spider is catching prey at night and sitting on its dwelling plant, its behaviour is largely guided by its **vibration sense** and its air movement sense. Here, a male *C. salei* is seen sitting on his plant (modified from Barth 2002) assuming a posture which tells the expert "I am ready for prey capture". With its body slightly raised and the legs spread out evenly around its body, the spider will respond to the slightest vibration of the plant generated by a prey insect (like an earwig or a cockroach) running around on the plant. Arrows point to the position of the vibration detectors (metatarsal lyriform organs) on the distal end of the metatarsus of all walking legs. The scanning electron micrograph (photograph by R. Müllan) shows such a vibration sensitive organ as seen when looking at the leg from above.

bration receptors and highly sensitive airflow receptors. Both senses are alien to our own experience. Their exquisite sensitivities in spiders are indeed remarkable.

The amplitude of the *substrate vibrations* produced by a cockroach walking around on a banana plant or a bromeliad may be as small as a millionth of a centimetre and still be sensed (Barth & Geethabali 1982). It is important to measure such values experimentally. Together with knowledge about the intensity and the frequency components of the signals emitted by the sender and the transmission properties of the plant they tell us the range of the vibratory signals in a spider's sensory world. This range measures several metres. The record found in an experiment done at the OTS station in Las Cruces, Costa Rica was 3.8 m. Under optimal conditions it may be even more. Not surprisingly then, the spider vibration receptors are among the most sensitive vibration receptors in the animal kingdom. They are called metatarsal lyriform organs for the following reasons: (i) they are located on the distal ends of the metatarsi of all walking legs and (ii) they represent strain detectors consisting of tiny innervated slits in the cuticle, arranged in parallel and therefore called lyriform slit sense organs because of a superficial similarity with the musical instrument (Fig. 7) (for a review see Barth 2001, 2002). When the tarsus is moved up and down by the plant vibrations it presses against the distal end of the metatarsus compressing the sensory slits. This is the stimulus the slits respond to with the generation of nervous signals.

An interesting feature of the 21 slits composing a metatarsal organ is their relative insensitivity to low frequencies (up to roughly 20 to 40 Hz). Such low frequencies are typical of background vibrations like those produced by the wind. The consequence is an increase of the signal to noise ratio which helps the spider to distinguish between biologically irrelevant vibrations of abiotic origin and the behaviourally relevant vibrations like those produced by the cockroach while running around on the plant. Very recent experiments revealed that the high-pass filtering properties of the organ just described are largely due to a clever "engineering" trick: the viscous properties of a cuticular pad between the tarsus and the vibration sensitive slits are such that the pad transmits more energy (absorbs less) at high frequencies than at low frequencies (McConney et al. 2007). This is a perfect case to demonstrate the intimate relationship between environment, filtering in the sensory periphery, and behaviour.

Courtship behaviour

Like prey capture, reproduction is of fundamental importance for *Cupiennius*, as it is for other animals. The vibration sense again is of prominent importance: much of the flirtation and communication between the sexes is by vibration signals (Fig. 8), which (unlike visual signals) also function at night.

Cupiennius males and females spend less than one hour of their lifetime (the large species reach an age of about two years in the laboratory) together. After that, they again go their separate ways. Their brief meeting, however, is full of ingenious mechanisms ensuring reproduction. The plant, which serves as a signal-transmitting channel, is the most important environmental
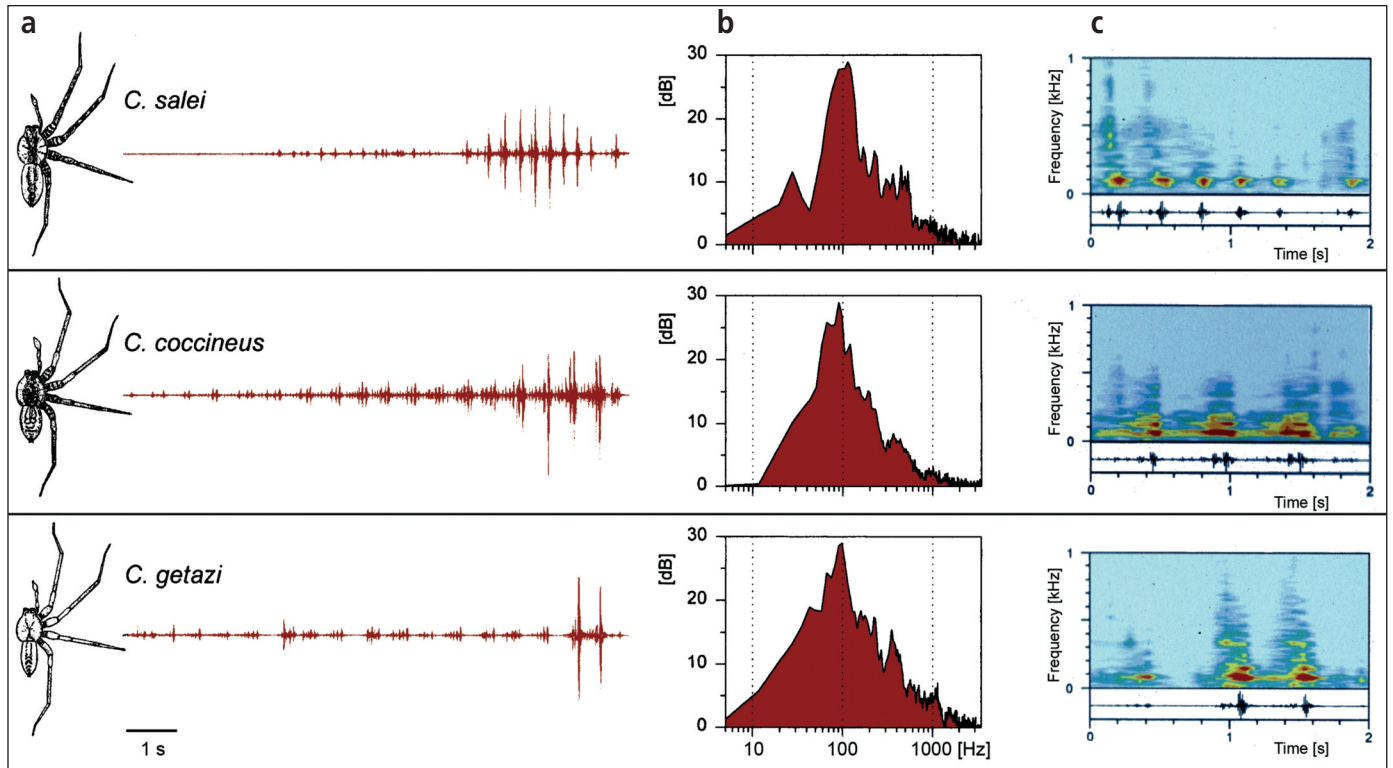
Fig. 8: **Vibratory communication** between the sexual partners plays a dominant role in the courtship behaviour of *Cupiennius*. The vibrations of the males are of prime importance for the reproductive isolation of the species. It is mainly the temporal pattern which differs among the species. A female responds to conspecific courtship vibrations with high preference. (**a**) Plant vibrations produced by the males of the three large species of *Cupiennius*. (**b**) Frequency spectra of the courtship vibrations showing impressive similarity. (**c**) Vibrograms showing the frequency contents of the vibratory signals as a function of time. The differences in temporal pattern are obvious. Different colours denote different intensity of frequency component, red indicating the strongest and light blue the weakest (left and middle row: modified from BARTH 2002).

factor. The elaborate courtship behaviour of *Cupiennius* fulfils a number of important functions which are shortly addressed in the following (for a review see BARTH 2001, 2002 and 2004).

The female initiates the communication by attaching a pheromone to her dragline or safety line which she always leaves where she walks. A rare case in spiders, this pheromone has been identified as S-dimethyl ester of citric acid in C. *salei* (TICHY et al. 2001). When the male spider wanders around at night and encounters such a female thread he will examine it with contact-chemosensitive hairs on his pedipalps (GINGL 1998, TICHY et al. 2001), recognise the presence of a female and start to introduce courtship vibrations into the plant by oscillating his opisthosoma and scratching the plant with his pedipalps (Fig. 8). In C. *salei*, the signal consists of a series of up to 50 syllables each of which in turn comprises up to 12 pulses. There is a distinct and species specific temporal structure in the signal, a syllable roughly lasting for 100 ms and the pause between two syllables for 250 ms. The most prominent frequencies the signal contains are between 75 Hz and 100 Hz. The pedipalp signals are considerably shorter and con-

tain higher frequencies, and are often omitted; they are not necessary for a normal and successful courtship (BAURECHT & BARTH 1992). The vibration-transmitting channel is again the plant. The signal loses about half of its amplitude after having travelled ca. 18 cm through bromeliads or agaves. But as we have seen the amplitude of the signal sent, its attenuation on the way to the female and the enormous sensitivity of the female vibration sensor taken together ensure a communication range of up to several metres. Provided the female receives a conspecific signal, she will answer with her own vibration. The female vibration signal is less structured temporally and composed of lower frequencies than that of the male. Its physical properties are well matched to the plant and therefore the female signal travels effectively to the male. Having received the female response, the male will approach the female during ongoing vibratory communication.

It should be noted that the female and male courtship signals have profoundly different functions.

(i) The female pheromone causes arousal and sexual excitation of the male, signalling the presence of a female.

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Tarsus **Metatarsus** **Tibia**
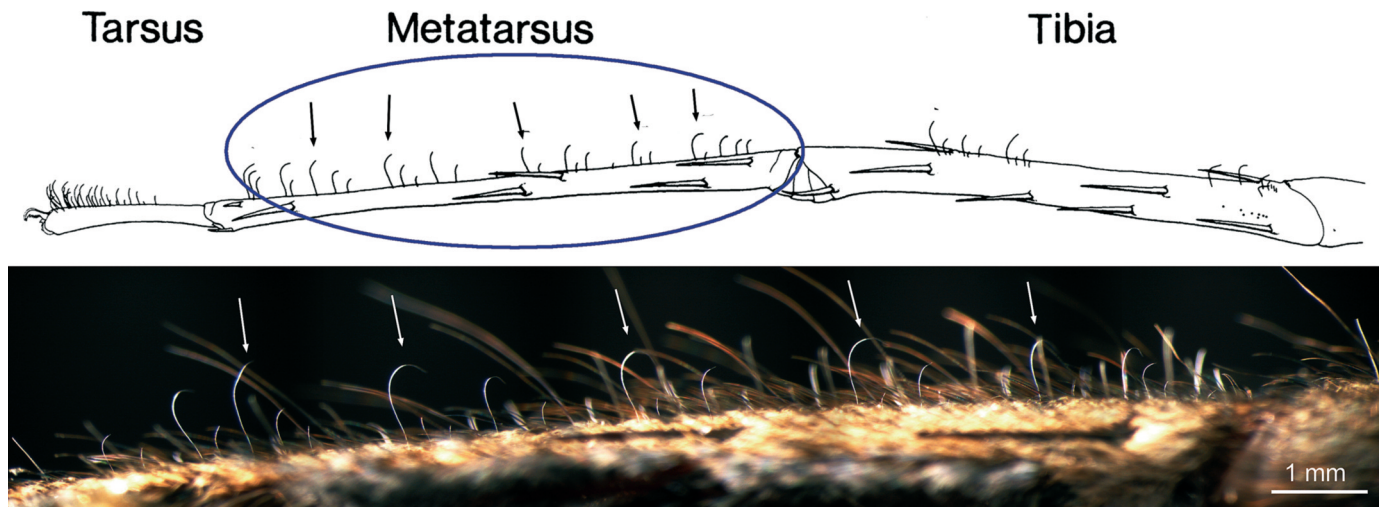
Fig. 9: **Air movement detection.** Apart from plant vibrations (see Fig. 7), air movements produced by a potential prey (in particular a flying one) help to guide the spider to its victim. The sensors involved are highly specialised fine hairs on the legs called trichobothria (see arrows) (photograph C. Schaber and C. Klopsch).

(ii) The male vibrations are highly species-specific (contrary to the female pheromone) in regard to their temporal pattern and serve the reproductive isolation of sympatric species which is mainly the task of the female (responds to conspecific signal with significant preference as compared to heterospecific *Cupiennius* signals).

(iii) Female vibrations indicate the presence of a conspecific partner to the male and guide him to the female.

Air flow detection

In contrast with orb-weaving spiders like *Nephila* (Fig. 12) or *Araneus*, which depend on web vibrations as indicators of an insect caught in their web, in *Cupiennius* and other wandering spiders, prey-catching behaviour can be elicited by air movements alone. In other words, alerted by air movements, a hungry spider will jump into the air to catch a flying insect. Again, extremely sensitive sensors are involved here, the so-called trichobothria (Fig. 9). These sensors are delicate hairs waving in the wind. They are lightweight structures and very flexibly articulated with the exoskeletal cuticle of the legs and pedipalps. They are between about 100 μm and 1400 μm long in *Cupiennius* and among the most sensitive sensors known in the animal kingdom. Regarding the number of trichobothria, *Cupiennius* seems to be the champion among all spiders so far examined with a total of about 950. Considering the extremely high absolute sensitivity of the trichobothria to air movement (that is the frictional forces exerted by the moving air particles) it follows that the interaction between the air and the hair must be a very intimate one and extremely well "engineered". This has been the topic of a considerable amount of biological and fluid mechanical research and mathematical modelling

(BARTH 2001, 2002; HUMPHREY et al. 2003; HUMPHREY & BARTH 2007), which is also relevant for technology with its increasing interest in bio-inspired sensors.

A few remarks will suffice here to demonstrate again the close relationship between sensory biology and ecology. The obvious question is why the spider doesn't jump into the air to catch the ever-present wind. One of the answers to this question is that after sunset, when *Cupiennius* leaves its retreat to sit on its dwelling plant waiting for prey, the air movement is much slower (typically below 1 m/s) than during daylight and much steadier (RMS values below 15%; dominant frequencies below 10 Hz). This implies that the nocturnal way of life is also an advantage for the detection of a prey-generated air flow signal and for its distinction from the inevitable background noise. The reason? A typical prey generated air flow like that of a fly, which readily elicits prey capture behaviour, reaches velocities of up to 1 m/s and the fluctuation values larger than 50% with frequencies as high as 100 Hz and more. A fly signal measured at a distance from the fly of about 25 or 30 cm closely resembles the background wind … and the spider does not react to it anymore. Like in case of the substrate vibration detector, the physiological properties of the trichobothria are finely tuned to the properties of the biologically relevant signals (see review in BARTH 2001, 2002).

Vision

When considering spider vision, the species one first thinks of are jumping spiders (Salticidae) like *Portia* or the ogre-faced spider *Dinopis* (Dinopidae) (Fig. 10). They are the masters of visual perfection. Day active *Portia*, in particular, is famous for outstanding spatial resolution (2.4 min, which is 10 times better than in the dragonfly,

Fig. 10: One of the most spectacular spiders (although looking like an inconspicuous twig) in the Golfo Dulce region is *Dinopis*. Among arachnologists it is well known both for its extremely sensitive night vision and its peculiar way of actively using its web for prey capture. Above: The spider, a long-legged specialised orb weaver, spins a frame of smooth threads into which it places roughly in parallel dense and sticky ("woolly") silk. Below: Prepared to catch prey, *Dinopis*, a web-throwing spider, hanging from its safety thread, holds the snare with the tips of its first and second legs. When prey is approaching, the highly elastic web is considerably extended by spreading the legs, thrown over the prey and then reduced in size again by loosening the tension. Thus the prey quickly becomes entangled.

the "best" insect) (Labhardt & Nilsson 1995; Land 1997; Land & Nilsson 2002). Night active *Dinopis* with its peculiar way of catching prey by throwing its web at its insect prey (which I had the good fortune to observe for a long night in the OTS Wilson gardens of Las Cruces, Coto Brus; Fig. 10), has photoreceptor cells responding half maximally at light intensities between starlight and moonlight (Laughlin et al. 1980).

How about *Cupiennius*? Despite the dominance of the mechanical senses in the behaviour of *Cupiennius*, its eight eyes and their visual brain centres are well developed (see review in Barth 2001, 2002). Like in oth-er spiders, the arrangement of the eyes on the prosoma is an important diagnostic feature for the taxonomic identification of *Cupiennius*. Fortunately for the field biologist, it clearly differs from that of closely related families like the Lycosidae and Clubionidae, and also from that of most of the Pisauridae. In the field, it is useful to know that no other taxonomically related genus or family has eight truly circular eyes like *Cupiennius* (instead of oval or kidney-shaped ones) (Fig. 11).

The quality of the image-producing optical apparatus of the eyes is excellent (Land & Barth 1992). The sensitivity of the sensory cells – as judged from their

Fig. 11: Left: In *Cupiennius,* the lenses of all of the **eight eyes** are perfectly circular as seen from outside. In addition to the pattern formed by the eye arrangement, this is a very reliable cue to quickly decide in the field whether a spider belongs to the genus or not. Right: When searching for *Cupiennius* at night, it is important to know their dwelling plants. To find them actually sitting on such a plant one often is reliably guided by the reflection of the flashlight from the tapeta of its secondary eyes as seen in this photograph.

structure – is high and closely correlates with ecology, that is the darkness of the nocturnal environment (GRUSCH et al. 1997). Electrophysiological experiments support this conclusion (BARTH et al. 1993; WALLA et al. 1996). The most recent electrophysiological analysis (PIRHOFER-WALZL et al. 2007) demonstrated long integration times of the photoreceptor cells and large responses to single photons in the dark-adapted state. These features improve visual reliability in dim light and contribute to the high visual sensitivity of *Cupiennius* at night. The price to be paid is slowness of vision. This would be fatal for fast flying insects, but like the toad, *Cupiennius* is a sit-and-wait hunter and can afford to sacrifice temporal resolution for absolute sensitivity (PIRHOFER-WALZL et al. 2007).

When searching for *Cupiennius* at night, a biologist should mainly be guided by their dwelling plants. A helpful additional clue is provided by the tapetum present in six of the eight eyes. The tapetum not only helps the eyes to increase their photon catch but it also reflects the light of a searching flashlight and thus reveals the spider's position (Fig. 11).

Does *Cupiennius* see colour? Considering the spectral sensitivities of its photoreceptor cells this is a possibility. Behavioural experiments, however, show that (similar to the honey bee) at least for vision of moving objects no colour sense is involved (ORLANDO & SCHMID, in preparation).

Both prey capture and courtship are not obviously disturbed when all eyes are covered by the experimenter. How then does *Cupiennius* make use of its visual potential in behaviour? A lot still has to be learned. One behaviour well demonstrated to use vision is the discrimination of visual targets. There is a preference for a vertical bar to a tilted bar (SCHMID 1998). In the field at night we repeatedly watched spiders walking straight to the pseudostem of a banana plant or else towards one of our trouser legs. According to experimental evidence the anterior-median (AM) eyes and the posterior median (PM) eyes play different roles: AM eyes are needed for discrimination among different targets, whereas the PM eyes merely detect their presence. We suppose that particularly the males, which wander around at night and are the true wandering spiders, use their vision to locate plants on which they will find females, prey, and/or a suitable retreat.

Again and again we see that there is no sense of senses without ecology and behaviour.

Epilogue

A systematic search for the spiders living in the Golfo Dulce region is overdue and the harvest awaiting the arachnologists can safely be predicted to be a rich one. Among the finds will be a number of species of *Cupiennius* (a genus typical of the Central American arachnofauna), in addition to those already known to occur in this area of fascinating biological diversity.
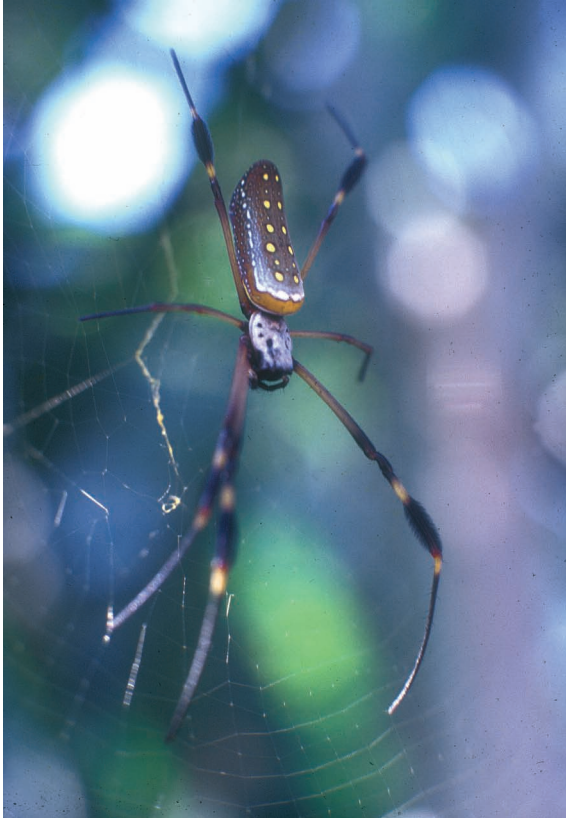
Fig. 12: *Nephila clavipes,* the golden silk spider belongs to the most beautiful spiders of the New World tropics. Its orb web reaches diameters of 1.5 m and more. The web is a mechanically particularly strong web which can be used by the spider for long periods of time without being taken down and built again daily as other orb weavers do. A peculiarity of *Nephila* is the enormous size dimorphism. The photograph on the right shows the tiny male copulating with the much larger female.

Concentrating on this genus, the present review aimed to give a flavour of the complex and intimate relationships between ecology, sensory systems, and behaviour and of the rewards of an integrative and organismic approach to animal biology.

The sensory world of *Cupiennius* is small, extending not further than a few metres. There are no long-distance senses like our eyes and ears which so much dominate the human sensory experiences. Clearly, the spider world is a rich world, albeit very different from ours. *Cupiennius* teaches us to see in what detail senses and behaviour reflect the properties of the environment. We recognise a fascinating adaptedness to the biologically relevant needs of the spiders in their specific habitat which is dominated by the close relationship to their dwelling plants. We become aware of the "cleverness" in the sensory periphery which is one of the reasons why animals with such small brains exhibit such complex behaviour. By studying this adaptedness we learn a lot about the habitat as well, and at the same time increasingly appreciate and love it.

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